

ULTRASTRUCTURE OF THE CHORION OF *DIOTRIA FLAVIPENNIS* MEIGEN, 1820 (DIPTERA: ASILIDAE: STENOPOGONINAE) COMPARED WITH THOSE OF FOURTEEN ASILID SPECIES FROM THE MID-ATLANTIC REGION OF NORTH AMERICA

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Abstract.—The fine structure of egg morphology of *Dioctria flavipennis* Meigen 1820 was studied utilizing both scanning electron (SEM) and transmission (TEM) microscopy. Eggs from Aksaray, Turkey, averaged 0.4 mm in length and 0.3 mm in width and had a single micropylar opening at one end. Chorions were covered with small and large circular elevated structures. A micropylar region eclosion groove is reported for the first time. Sperm flagella were present in the micropylar region of some eggs. The endochorion and exochorion were distinguished from each other in TEM micrographs, the former being slighter more dense than the latter. Lamellar sheets, minute canals, and air ducts were also found. Additionally, the exochorion of the egg of *D. flavipennis* was compared with those (SEMs) of 14 asilid species from the mid-Atlantic region of North America: *Atomosia puella* (Wiedemann), *Cerotainia albipilosa* Curran, *Eudioctria tibialis* (Banks), *Holcocephala abdominalis* (Say), *H. calva* (Loew), *Laphria divisor* (Banks), *L. flavicollis* Say, *L. ithyphi* McAtee, *L. sicula* McAtee, *L. virginica* (Banks), *Leptogaster flavipes* Loew, *Psilonyx annulatus* (Say), *Tipulogaster glabrata* (Wiedemann), and *Tolmerus* sp. Brief comments about the phylogeny of the egg chorion and its adaptation to various environmental conditions are included. Egg morphology may be useful to elucidate taxonomic and phylogenetic relationships among asilids.

Key Words: egg morphology, ultrastructure, chorion, *Dioctria flavipennis*, Asilidae, Diptera, SEM, TEM

The taxonomic importance of egg morphology has become increasingly significant in a wide variety of insect orders, such as Diptera (Lounibos et al. 1997), Lepidoptera (Salkeld 1983, 1984; Suludere 1988), Hemiptera (Javahery 1994), and Pleocoptera (Szczytko and Stewart 1976, Starks and Stewart 1981). The surface structure of dipteran eggs, as revealed by scanning electron microscopy (SEM), often provide reliable

characters for separating species (Salkeld 1980, Kula 1988, Kuznetsov 1988, Linley and Chadee 1990, Sahlen 1990, Mouzaki et al. 1991, Feliciangeli et al. 1993, Greenberg and Singh 1995, Service et al. 1997, Suludere et al. 2000a, b). Although an extensive survey of respiratory and morphological structures of insect eggs have been conducted by Hinton (1981) and Margaritis (1985), little information concerning the

Table 1. Summary of descriptions of asilid eggs (Diptera) using SEM microscopy.

Subfamily and Species	Citation
LEPTOGASTRINAE	
<i>Psilonyx annulatus</i> (Say)	Castillo et al. 1994
STENOPOGONIAE	
<i>Archilestroides quimaraenis</i> (Artigas and Papavero 1991)	Castillo et al. 1994
<i>Taperigma diomitiformis</i> Artigas and Papavero 1991	Castillo et al. 1994
DASYPOGONINAE	
<i>Megapoda labitata</i> (Fabricius)	Castillo et al. 1994
LAPHRIINAE	
<i>Atomosia dasypus</i> (Wiedemann 1828) as <i>Paratractia dasypus</i>	Castillo et al. 1994
<i>Andrenosoma atra</i> Linnaeus 1758	Musso 1981
<i>Andrenosoma bayardi</i> (Seguy 1952)	Musso 1981
<i>Dissmeryngodes anticus</i> (Wiedemann 1828)	Castillo et al. 1994
ASILINAE	
<i>Antipalus varipes</i> (Meigen 1820)	Musso 1981
<i>Cnodalomyia</i> sp.	Castillo et al. 1994
<i>Colepia abludo</i> (Daniels 1983) as <i>Neoaratus abludo</i> Daniels	Lawson and Lavigne 1984
<i>Dystolmus kiesenwetteri</i> (Loew 1854) as <i>Eutolmus kiesenwetteri</i> Loew	Musso 1981
<i>Machimus fimbriatus</i> (Meigen 1820)	Musso 1981
<i>Machimus fimbriatus</i> (Meigen 1820)	Suludere et al. 2000a
<i>Machimus pilipes</i> (Meigen 1820)	Musso 1981

surface structure of eggs of Asilidae was reported by these authors. Many papers that cover robber fly reproductive behavior include a superficial description of the eggs (e.g., Dennis 1979; Lavigne 1963a, b, 1964).

Previous detailed published SEM studies of the external morphology of asilid eggs are summarized in Table 1. In this study, we examined the egg structure of *Dioctria flavipennis* Meigen 1820 in detail utilizing both scanning (SEM) and transmission electron (TEM) microscopy to extend our knowledge of egg surface structures that might be utilized in the taxonomy of the Asilidae in the future. Additionally, the exochorion of the egg of *D. flavipennis* was compared with those (SEMs) of 14 asilid species from the mid-Atlantic region of North America: *Atomosia puella* (Wiedemann 1828), *Cerotainia albipilosa* Curran 1930, *Eudioctria tibialis* (Banks 1917), *Holcocephala abdominalis* (Say 1823), *H. calva* (Loew 1872), *Laphria divisor* (Banks 1917), *L. flavicollis* Say 1824, *L. ithyphi*

McAtee 1919, *L. sicula* McAtee 1919, *L. virginica* (Banks 1917), *Leptogaster flavipes* Loew 1862, *Psilonyx annulatus* (Say 1823), *Tipulogaster glabrata* (Wiedemann 1828), and *Tolmerus* sp.

MATERIAL AND METHODS

Eggs were obtained from ovipositions by females of *Dioctria flavipennis* collected in Aksaray, Turkey (14.vi.1998). Females deposited eggs singly on cotton batting in plastic jars. The eggs were gently removed from the cotton fibers and prepared for scanning electron microscopy (SEM) following standard methodology (see Suludere 1988). Eggs were mounted with double-sided tape on SEM stubs, coated with gold in a Polaron SC 502 Sputter Coater, and examined with a JEOL JSM 5600 Scanning Electron Microscope at 10 kV. Eggs of 14 asilid species from the mid-Atlantic region of North America were treated similarly, except that the Leptogastrine eggs were freeze-dried before coating with gold. Eggs prepared for examination under Transmis-

sion Electron Microscope (TEM) were fixed with 2.5% glutaraldehyde in a phosphate buffer (pH 7.2) for 2 hours and post-fixed with 1% osmium tetroxide in a phosphate buffer (pH 7.2) for 1 hour. The samples were embedded in Glauert's araldite medium and the ultrathin sections were stained with Reynold's lead citrate following uranyl acetate. These eggs were examined with a Zeiss EM 900 Transmission Electron Microscope at 80 kV.

RESULTS

Eggs of *Dioctria flavipennis* are ovoid, dull brown, and approximately 0.4 mm in length and 0.3 mm in width (Figs. 1, 2). The exochorion is covered by erect, relatively thin, oval rings of varying sizes (Figs. 3–6). The walls of these structures are curved, appearing crown or cup-shaped in lateral and dorsal views (Figs. 3, 4, 8). Aeropyles are present on the floor of these structures and occasionally outside of them (Figs. 4, 6). One end of the egg [micropylar region] is fairly smooth, contains one micropyle, and is surrounded on its outer edge by irregularly spaced, cup-like structures and a row of larger, oval rings (Figs. 1, 3, 7). An eclosion groove is visible between the two latter structures, delineating the micropylar region from the remaining exochorion (Figs. 3, 4). Larvae emerge from eggs by pressing against the micropylar region [operculum], causing it to separate along the thin, weaker eclosion line (Fig. 2). Sperm flagella are sometimes present in the micropylar area (Figs. 7, 22).

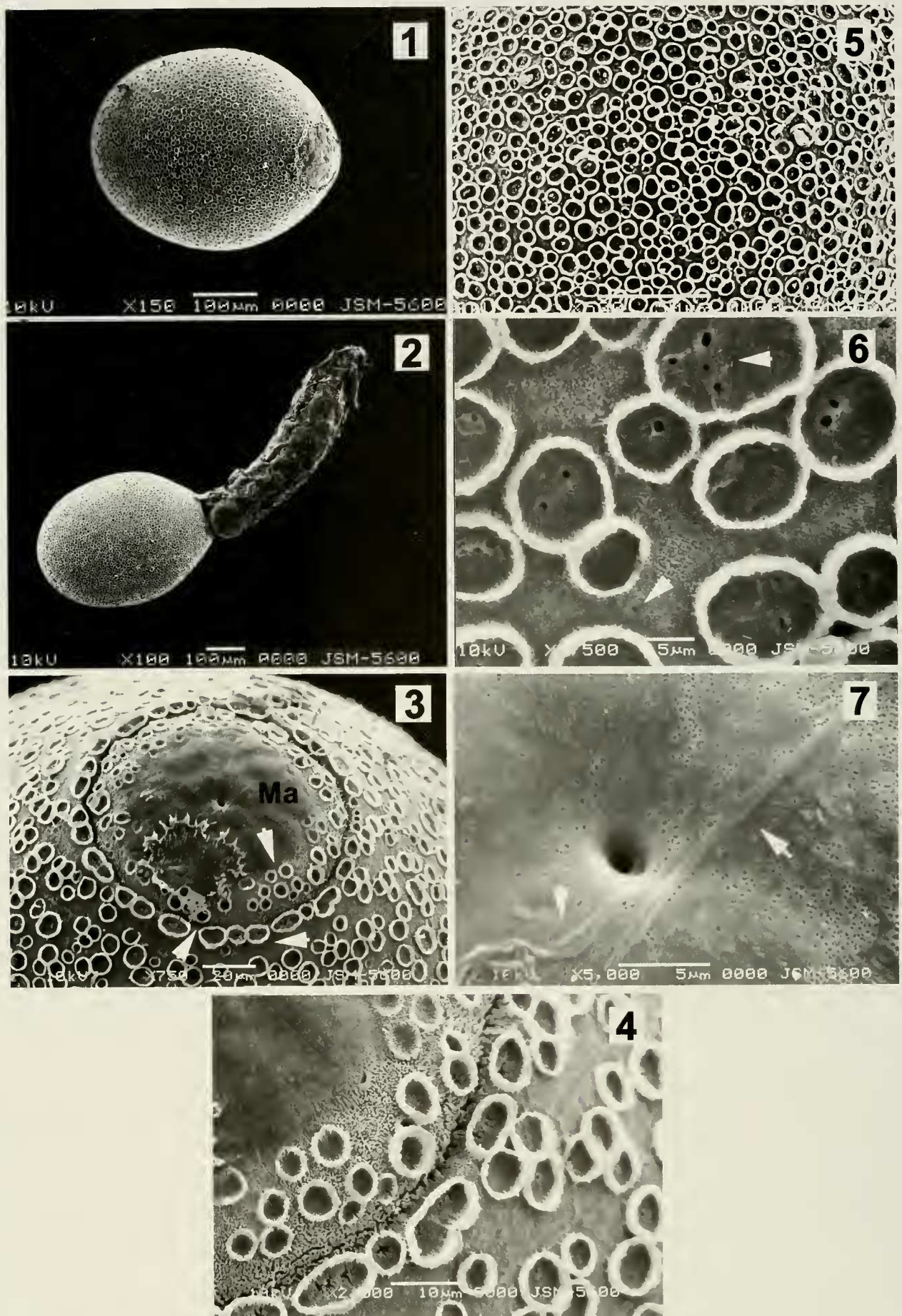
The chorion of *Dioctria flavipennis* is composed of two layers, each of which is composed of lamellar sheets, minute vertical canals, and small cavities that probably connect to the surface aeropyles (Fig. 8). The electron density of the endochorion, which rests on the vitelline membrane, appears more compact than that of the exochorion. The latter appears somewhat rippled or rugose in cross-section near the outer surface due to the presence of rather large horizontal chambers or grooves. The

exochorion is covered externally with a thin, nonstratified material, possibly wax (Fig. 8). The broken edge of the chorion of *L. divisor* suggests a more complex organization of lamellar bundles, angled in a crossing pattern, which would enhance the tensile strength of the endocuticle along its inner surface (Fig. 9).

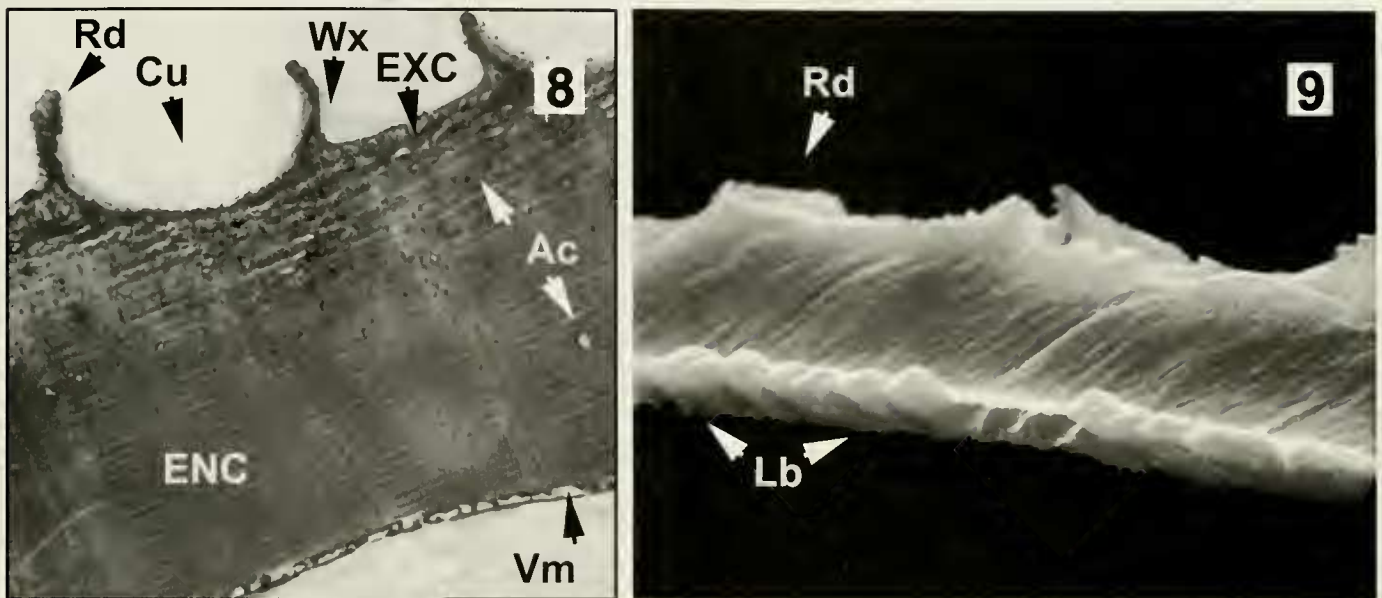
The egg morphology of the mid-Atlantic North American species differs from that of *Dioctria flavipennis*. Two contrasting types of exochorions were found (Figs. 9–33). One with a simple, smooth exochorion (three Leptogastrinae and one Asilinae species) without erect exochorionic rings and aeropores (Table 2, Fig. 10) and a second with complex polygon rings and numerous, widely distributed, aeropyles (Laphriinae, Dioctriinae, and Trigonimiminae). Pentagon and hexagon shaped rings are most common. The polygon ridges are usually thicker and shorter than those in *D. flavipennis* (Figs. 8, 9, 14–21, 23, 27, 29, 33). The exceptions include *Laphria ithyphi* (Fig. 11–12), which has peglike tubercles connected at angles to unusually low ridges and *Holcocephala calva* (Figs. 13, 24), which has taller, thinner-walled rings. In most species, ridges are solid, either as a raised exochorion surface or formed of fused surface processes. Those of *Laphria flavicollis*, *Cerotainia albipilosa* and *Atomosia puella* are composed of loosely organized hairlike or thicker digitate processes (Figs. 17–19, 25).

The broad interridge areas are usually much shorter than the surrounding ridges and covered by erect processes. However, the interridge processes on eggs of *C. albipilosa* and *A. puella* are only slightly shorter than those that form the ridges (Figs. 17, 18). The interridge areas are sometimes bare (Figs. 15, 21), especially near the micropylar region (Fig. 23), but most are covered with various processes, of which some are fused whereas others are thin and hairlike or thicker and digitate (Figs. 16–20, 22, 23, 25).

Aeropyles are widespread across the ex-



Figs.1-7. Egg morphology of *Dioctria flavipennis*. 1, SEM micrograph of an unhatched egg. 2, SEM micrograph of an egg and emerging first instar larva. 3, SEM micrograph of the micropylar region [Ma] showing a micropyle, distribution of circular rings. Also note an ecllosion groove and a row of ovoid rings surrounding the micropylar region. 4, SEM micrograph of an ecllosion line and distribution of circular and ovoid rings. Note aeropyles on the floor of the ringed walls. 5, SEM micrograph showing the distribution of ovoid rings on the surface of the exochorion. 6, SEM micrograph showing the aeropyles on the floor of oval rings and on the general surface of the exochorion. 7, SEM micrograph of the micropylar region with a micropyle and a sperm flagellum.



Figs. 8–9. TEM and SEM micrographs of sections of egg chorions of *Dioctria flavipennis* and *Laphria divisor*, respectively. Abbr. Ae = air canals-chambers, Cu = cup-like exochoronic ring, ENC = endochorion, EXC = exochorion, Rd = exochoronic ridges, Vm = vitelline membrane, Wx = wax?.

ochorion surface, including both ridges and interridge areas, and are more numerous than those in *D. flavipennis* (Figs. 6, 17, 19–24, 30–32). They usually occur as single surface pores on flat surfaces, at the top of processes or cone-shaped elevations (Figs. 17, 19, 21–23, 25). Additionally, one to two clusters of aeropyles are present in each interridge area on the eggs of *Laphria sicula* (Fig. 20).

The micropylar area is largely smooth with ridges becoming shorter and flattened toward the center (Figs. 11, 27–29, 31–32). However, it is somewhat floral-like (Fig. 30) in *Holcocephala abdominalis* and weakly ridged in *Laphria flavicollis* (Fig. 33). An eclosion groove delineating the micropylar area is absent on eggs of all mid-Atlantic species in this study. Dual micropyles were found only in *Psilonyx annulatus* (Figs. 10–11, 26, 27–33, Table 2).

DISCUSSION

With the exception of the micropylar region, the surface of the chorion of *D. flavipennis* is covered with both small and large oval rings. Similar patterns were observed on the surface of eggs of certain *Dioctria* and *Laphria* species by Melin (1923) using a standard ocular microscope.

Scarborough (1978) reported finding “characteristic elevated ridges forming 4–7 sided rings with 6-sided rings being the most common” on the surface of eggs of *Cerotaenia albipilosa* Curran at 550× magnification, while Dennis (1979) illustrated hexagon rings on the surface of *Holcocephala fusca* eggs at 740× magnification. Dennis and Lavigne (1975) reported a “chorion smooth, without ornamentation” in six North American genera.

Musso (1981) studied the morphology and development of the immature stages of some European robber flies and classified the eggs into three groups: pigmented eggs, non-pigmented ones (ornamented and non-ornamented), and eggs covered with sand grains. He defined pigmented eggs as those, such as *Andrenosoma atra* and *A. bayardi*, which are colored and have a thick chorion composed of irregular juxtaposed polygon rings (pentagon and hexagon shaped). Unpigmented ornamented eggs, usually whitish, had a thick chorion covered by “nipples and tubercles surrounding numerous small cavities, crypts or crevices” as found in *Machimus fimbriatus*, and *Dystolmus kiesenwetteri*. He provided an SEM of *Machimus pilipes* to illustrate unpigmented non-ornamented egg and commented that *Mach-*

Table 2. Four egg characters present on 14 asilid species (Diptera) from the mid-Atlantic region of North America listed by subfamily.

Subfamily and Species	Chorion Surface	Aeropyles	Micropyle	Micropyle Area	Egg Shape
LEPTOGASTRINAE					
<i>Leptogaster flavipes</i> Loew*	thin, smooth w/o ridges	absent	one	smooth	oval
<i>Psilonyx annulatus</i> (Say)*	thin, smooth w/o ridges	absent	two	smooth	oval
<i>Tipulogaster glabrata</i> (Wiedemann)*	thin, smooth w/o ridges	absent	one	smooth	oval
TRIGONOMIMINAE					
<i>Holcocephala abdominalis</i> (Say)	thick, with thick, low uniform ridges	present	one	broad, floral-like	oval
<i>Holcocephala calva</i> (Loew)	thick, with tall thin uniform ridges	present	one	broad, smooth	oval
DIOCTRINAE					
<i>Eudictoria tibialis</i> (Banks)	thick, with thick low uniform ridges	present	one	broad, smooth	oval
LAPHRIINAE					
<i>Atomosia puella</i> (Wiedemann)	thick, with low uniform ridges	present	one	broad, smooth	oval
<i>Cerotantia albipilosa</i> Curran	thick, with low uniform ridges	present	one	broad, smooth	oval
<i>Laphria divisor</i> (Banks)	thick, with thick low uniform ridges	present	one	broad, smooth	oval
<i>Laphria flavicollis</i> (Say)	thick, with thick low uniform ridges	present	one	narrow with low ridges	oval
<i>Laphria ithyphi</i> McAtee	tuberculate corners, low interconnecting ridges	present	one	broad, smooth	elongate, ends bluntly rounded
<i>Laphria sicula</i> McAtee	thick, with thick low uniform ridges	present	one	broad, smooth	oval
<i>Laphria virginica</i> (Banks)	thick, with thick low uniform ridges	present	one	broad, smooth	oval
ASILINAE					
<i>Tolmerus</i> sp.*	thin, smooth w/o ridges	absent	one ?	smooth	elongate, narrow

* Chorion surface smooth and without obvious aeropyles as in *Psilonyx annulatus* (Say).

imus rusticus had the same surface characters. SEMs of the latter species taken by Suludere et al. (2000a) confirmed Musso's statement. Interestingly, the same exochorionic pattern is found on the eggs of *Asilus crabroniformis* (Clements and Skidmore 1998), being made up of globular masses of varying size. None of the eggs in our paper fall into Musso's third grouping: exochorion "entirely covered with a thin pellicle made of tiny (10–150 μ m) sand grains." The egg of *Antipalus varipes* is the only species that is known to have this type of exochorionic pattern.

Eggs of *Dioctria flavipennis* do not fall into any of these groups. Neither do their chorionic reticulations resemble any of those reported by Castillo et al. (1994). Only two species in the latter study can be placed in Musso's pigmented eggs category (*Dissmeryngodes anticus* and *Taperigna diogmitiformis*). Lastly, the chorionic structures on the eggs of *Colepia abludo* (Lawson and Lavigne 1984) also do not conform to any of Musso's groupings, nor do they equate with those of *D. flavipennis*. However, eggs of the mid-Atlantic North American species of Dioctrinae, Laphriinae, and Trigonimiminae can be placed in Musso's first grouping of pigmented eggs with thick chorions and juxtaposed polygons.

The micropylar area of an asilid egg is usually smooth and flattened around the micropyle. This study reports the first finding of a distinct single row of similar sized oval rings surrounding the micropylar region and an eclosion groove in *Dioctria flavipennis*. Both of the structures are absent in the American and European species thus far studied.

Our study also reports a single micropylar opening at the apex of the *D. flavipennis* egg. Lawson and Lavigne (1984) also reported sperm flagella in the micropylar opening of an egg of *Colepia abludo*. Sperm flagella are also reported near the entrance to the micropyle of *Holcocephala abdominalis* eggs (Fig. 30). That the micropylar opening is a central canal for the pas-

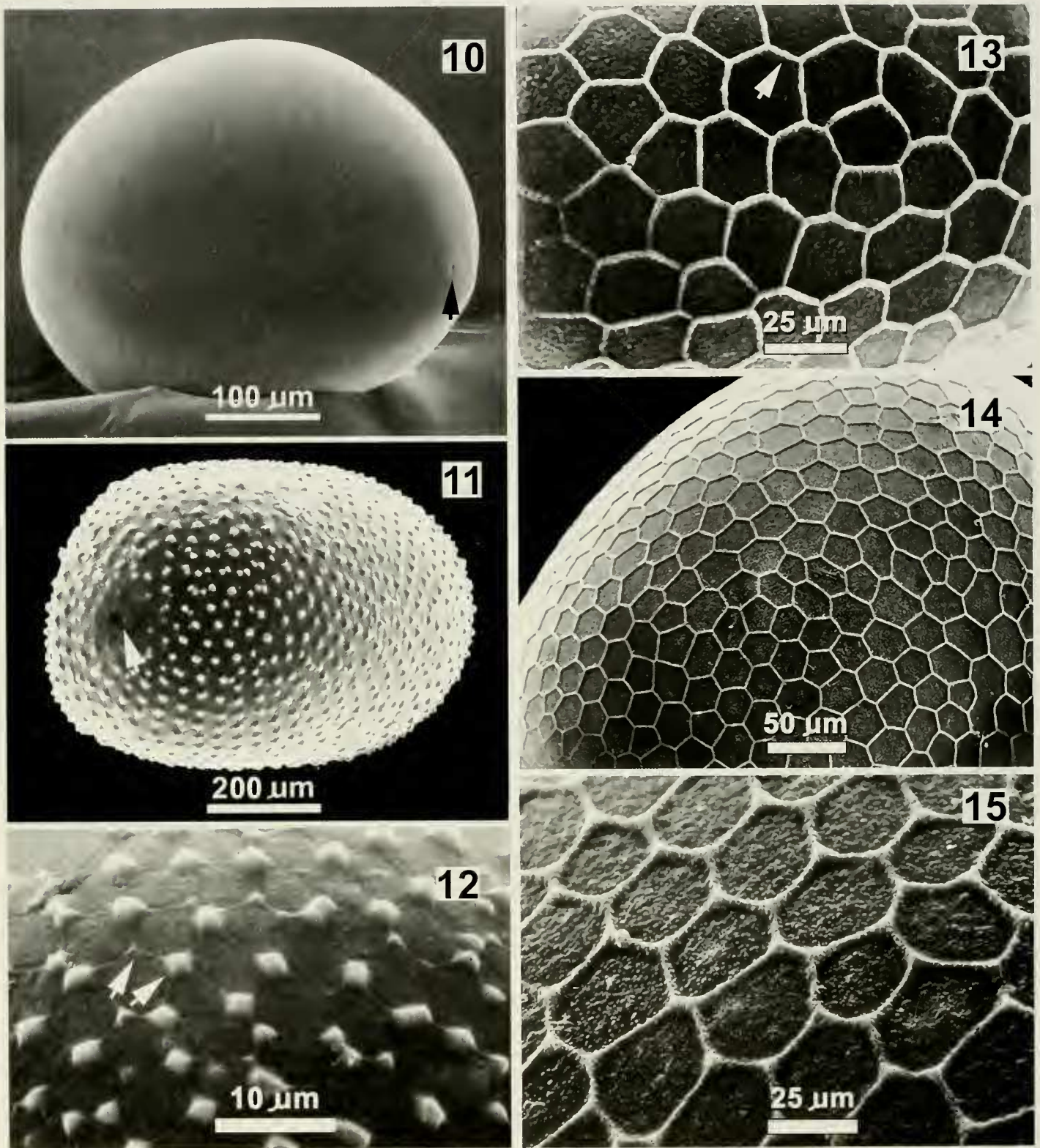
sage of sperm is also suggested by the presence of a single micropyle in the eggs of *Cnodolomyia* sp., *Archilestroides guimaraensis* and *Megapoda labiata* (Castillo et al. 1994) and most mid-Atlantic North American species, (Table 2, Figs. 19–24) with one exception. Interestingly, the eggs of *Atomosia dasypus* (Castillo et al. 1994) and *Psilonyx annulatus* (Table 2, Figs. 19–24) have two micropyles. Castillo et al. (1994) record dual micropyles for *Taperigna diogmitiformis*, but this is not apparent in their Figure 24, which shows only a single micropyle.

Conversely, no micropyle was found in *Machimus rusticus* eggs (Suludere et al. 2000a), nor was any noted on the exochorion of the eggs of *Asilus crabroniformis* (Clements and Skidmore 1998). Note, too, that Castillo et al. (1994) did not observe a micropylar opening in eggs of *Dissmeryngodes anticus*.

Suludere et al. (2000a) referred to the area at the end of eggs of *Machimus rusticus* as a micropylar region (anterior pole). She postulated that the openings of dome-like projections might be aeromicropylar openings through which sperm enter the egg. Similar multiple openings [aeropyles of Castillo et al. (1994)] are also seen in the exochorionic structures of *Holcocephala abdominalis* (Fig. 30), *Holcocephala calva* (Fig. 31), and *Eudioctria tibialis* (Fig. 32). However, the latter species have a single, large micropyle as well and much smaller pores which probably function as openings for gas exchange.

Insect eggs require a large surface area in order to supply adequate quantities of oxygen for the developing embryo. Because of the presence of air spaces, as seen in cross section under TEM, the eggs of *D. flavipennis* are able to perform plastron respiration thus supplying enough oxygen without significant moisture loss. Hinton (1969) suggested that the chorion is so structured to minimize water loss.

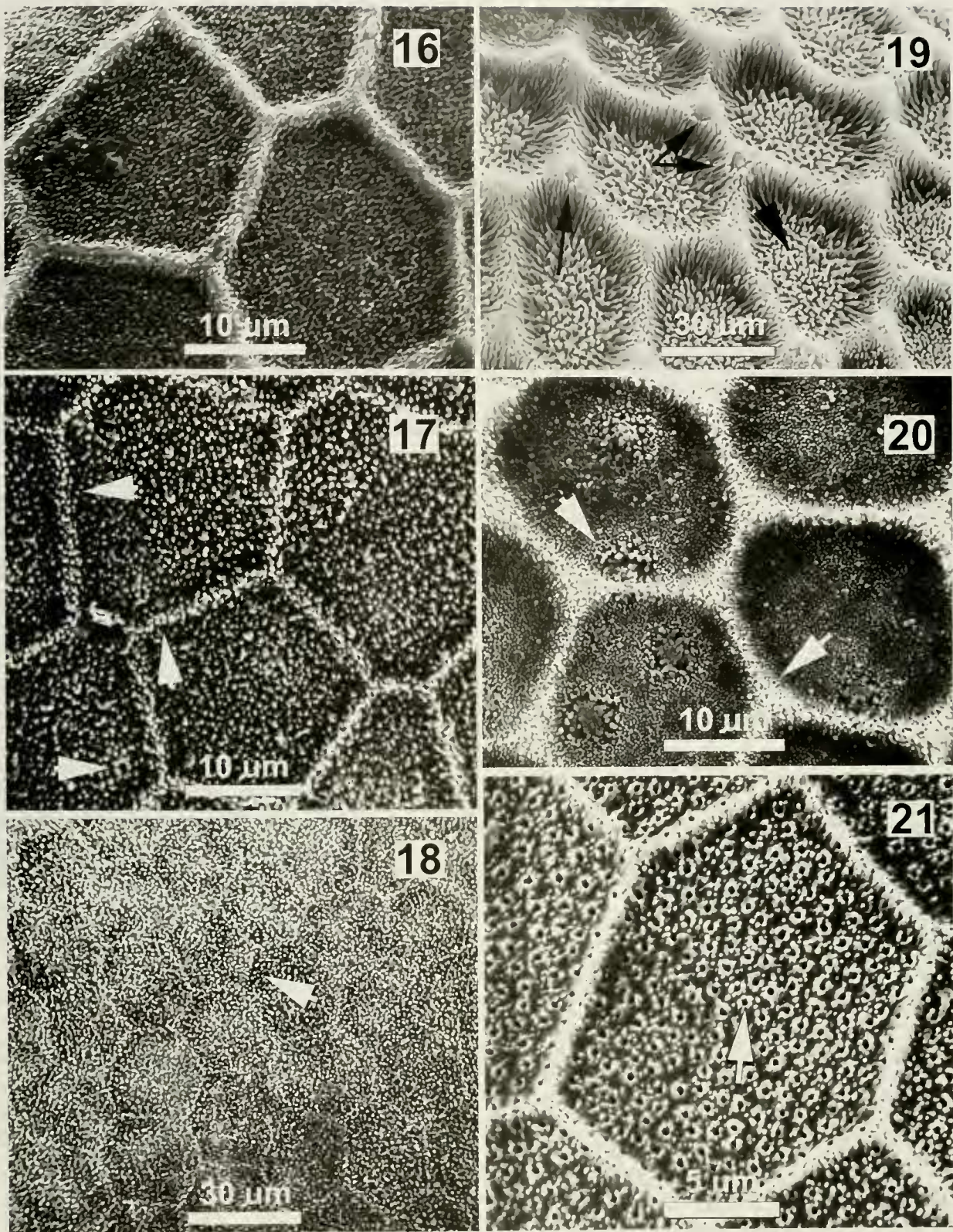
It is of interest taxonomically, then, that the exochorion of most Laphriine eggs have



Figs. 10–15. SEM micrographs of unhatched eggs of five asilid species from the mid-Atlantic region of North America. 10, *Psilouyx annulatus* showing a smooth chorion and micropyles [arrow]. 11–12, *Laphria ithygi* showing tuberculate pattern and unusually low interconnecting ridges and single micropyle. 13, *Holcocephala calva* showing tall, thin hexagon pattern. 14, *Eudioctria tibialis* showing hexagon ornamentation on the exochorion. 15, *Laphria divisor* showing hexagonal ornamentation on the exochorion.

pentagon-hexagon rings: Laphriinae—Atomosiini [*Atomosia puella* (Fig. 18), *Cerotainia albipilosa*, (Fig. 17) *Dissmeryngodes anticus* (Castillo et al. 1994)]; Laphriinae—Andrenosomini [*Andrenosoma atra* (Musso

1981), *Andrenosoma bayardi* (Musso 1981)]; Laphriinae—Laphriini [*Laphria divisor* (Fig. 15), *Laphria flavicollis* (Fig. 19), *Laphria sicula* (Fig. 20), *Laphria virginica* (Fig. 23)]. The exception is the egg of *La-*



Figs. 16–21. SEM micrographs of polygon patterns on the exochorion of six asilid species from the mid-Atlantic region of North America. 16, *Holcocephala abdominalis* showing thick, solid ridges. 17, *Cerotainia albipilosa* Curran showing low ridges formed from digitate processes and scattered aeropyles. 18, *Atomosia puella* showing unusually low polygon ridges. 19, *Laphria flavicollis* showing tall ridges formed from hair-like tubercles and distribution of aeropyles. 20, *Laphria sicula* showing thick ridges with the distribution of minute aeropyles on the general chorion surface, including ridges, and clusters of aeropyles in the interridge areas. 21, *Eudioctria tibialis* showing thick ridges and distribution of aeropyles. Note slightly elevated surface surrounding aeropyles.

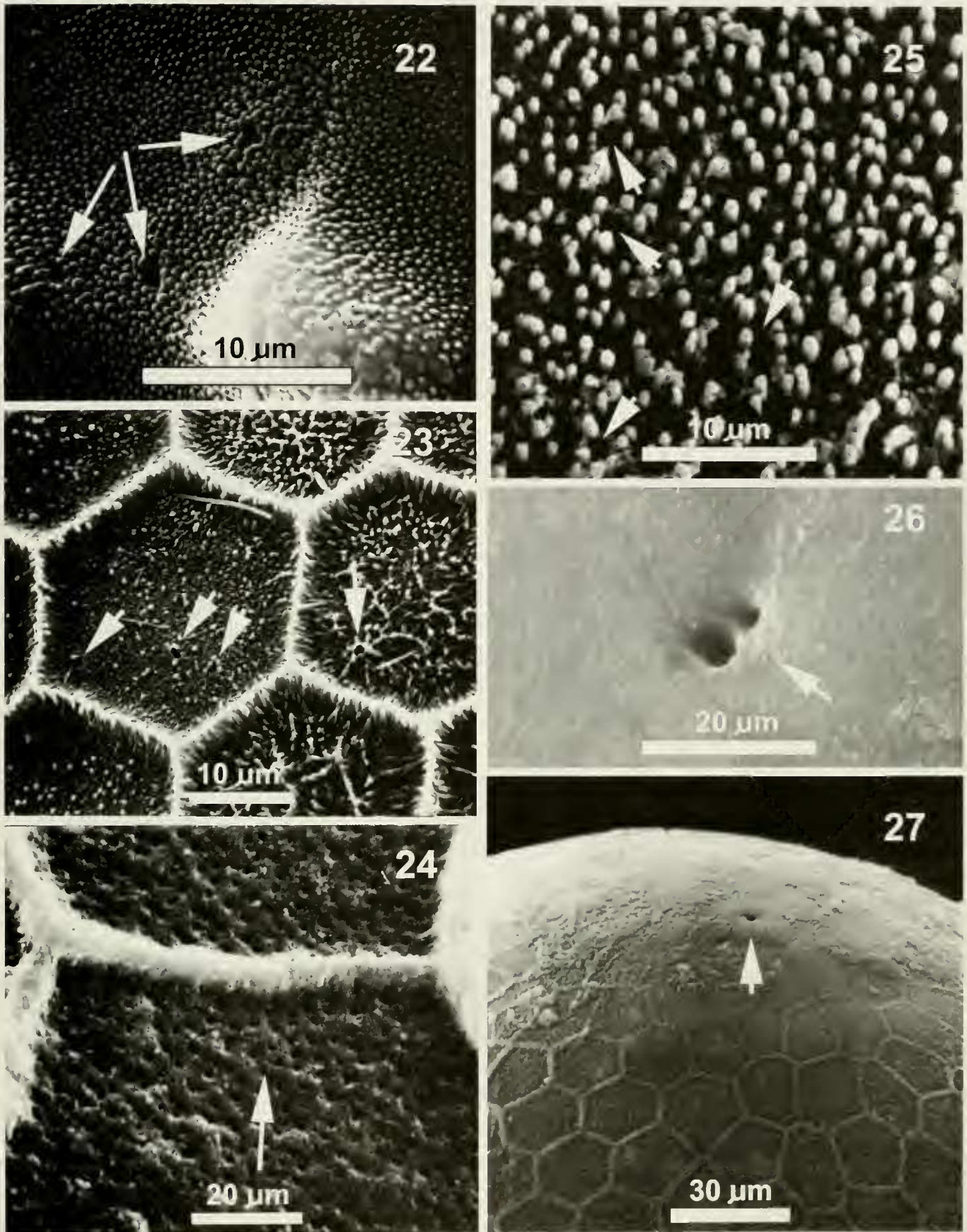
phria ithypgi (Figs. 11–12) that has rows of tubercles that appear to form slightly spiral rows at some angles, but corners of a pentagon or hexagon when viewed at a greater magnification. Hexagon rings also occur on the eggs of some Asilinae [*Cnodalomyia* sp. (Castillo et al. 1994)], on the eggs of some Dioctriinae—Echthodopini [*Eudioctria tibialis* (Fig. 14)] and on the eggs of some Trigonimiminae [*Holcocephala abdominalis* (Fig. 16), *H. calva* (Fig. 13)]. Conversely, the eggs of the Leptogastrinae [*Psilonyx annulatus* (Fig. 10), *Leptogaster flavipes* and *Tipulogaster badius* (Table 2)] are smooth, lacking any surface rings.

In this connection it is of interest to look at the phylogeny of the subfamilies of Asilidae, as portrayed by various authors. Hull (1962) considered that the Asilinae and Ommatiinae were the oldest with the Dasypogoninae (including the Stenopogoninae) being the youngest; whereas Lehr (1969) considered Dasypogoninae/Atomosiinae/Ommatiinae to be the oldest with Laphriinae and Megapodinae being the youngest. More recently, Papavero (1973) and Artigas and Papavero (1988) placed the Atomosiinae at the tribal rank (Atomosiini) in the Laphriinae and proposed that Ommatiinae, Apocleinae, Laphriinae and Laphystiinae were the youngest subfamilies, having been derived from the ancestor of the Asilinae, with the Leptogastrinae as an outgroup. However, Lehr (1991) maintained that Atomosiinae is a subfamily and suggests that it is the “most archaic group in the family” whereas Dasypogoninae/Trigonimiminae and Stichopogoninae/Stenopogoninae evolved about the same time as the Asilinae. It is therefore not surprising to find polygon exochorionic patterns occurring in only some Asilinae if the Laphriinae are indeed derived from the ancestor of Asilinae. The question is why did they disappear in some Asilinae species. It will be of considerable interest to look for exochorionic patterns on Dasypogoninae and Stichopogoninae/Stenopogoninae eggs.

Many asilids are forest-edge species

whereas few occur deep in forests. Species concentrated in this narrow, moist ecotone are subjected to intense competition for larval and adult food, developmental sites and predation from vertebrates that occupy or traverse this ecological zone. Further, most Asilinae+Apocleinae+Dasypogoninae and Stichopogoninae/Stenopogoninae species occupy a much wider ecotone, e.g. open grassy areas near forests, grasslands, savannahs, and deserts-dunes. Here species possibly exploit a broader, seasonally abundant food while reducing competition for developmental sites and larval food by dispersing eggs over wider areas. Further, vertebrate predators are likely less abundant and more widely dispersed which would reduce interactions between predators and larval and adult populations, e.g. reduce losses.

Asilid egg chorions are either thin-walled, smooth externally, and without aeropyles or thick-walled, sculptured externally, and with aeropyles. Each type can be associated with physiographic conditions of the environment, ovipositor type, and oviposition behavior. The transition from forest-edge to arid conditions ranges from moist to extremely dry, the deserts and sandy dunes being quite harsh. The forest-edge species have simple ovipositors and behaviorally drop their eggs at random [some Laphriinae being exceptions in that they drop eggs on or in cavities of decaying trees stumps and logs]. Eggs deposited in this manner are frequently, but temporally, inundated with water. Sculptured chorions with aeropyles trap gas bubbles on their surfaces that facilitates gas exchange [plastron respiration, e.g. the Laphriinae, Ommatiinae, Dioctriinae—Echthodopini *Eudioctria tibialis* and the eggs of some Trigonimiminae such as *Holcocephala abdominalis* and *H. calva*]. Additionally, North American *Dioctria* [including *D. baumbaueri* which presumably has been introduced from Europe], *Eudioctria*, and some Oriental *Damalis* species (Scarborough, unpublished data) have hexagon



Figs. 22–27. SEM micrographs of exochorion morphology of six asilid species from the mid-Atlantic region of North America. 22, *Laphria ithypgi* showing aeropyles. 23, *Laphria virginica* showing coned and coneless aeropyles. 24, *Holcocephala calva* showing coneless aeropyles. 25, *Atomosia puella* showing aeropyles surrounded by white-tipped tubercles. 26, *Psilonyx annulatus* showing dual micropyles. 27, *Cerotainia albipilosa* showing a single micropyle.

chorionic rings readily visible with light microscopy.

A second group has smooth chorions without aeropyles, e.g. Leptogastrinae, some Asilinae+Apocleinae+Dasypogoninae and Stichopogoninae/Stenopogoninae. Species of Leptogastrinae also drop their eggs at random (Dennis and Lavigne 1976), whereas those remaining groups have more selective oviposition habits. Interestingly, the latter (Martin 1968) are found within the grass zone of forest-edges in eastern North America and scrub vegetation in the Caribbean Islands (Scarborough, unpublished data) and in open grassland in western N. A. (Lavigne, unpublished data). Bybee et al. (2004), based on a molecular study, suggest that Leptogastrines are basal to all other asilid subfamilies.

Those asilids that have adapted to drier habitats also have thin-walled eggs with smooth surfaces and specialized behaviors and/or ovipositors. The latter have spines for digging and placing eggs in the soil or flattened ovipositors for inserting eggs into plant tissues or behind plant parts. Sand grains readily adhere to the chorions of *Proctacanthus* and *Ospriocerus* (Dennis and Lavigne 1975) when excavated, suggesting a sticky material is present. Many grassland and desert *Mallophora*, *Megaphorus* and *Promachus* (Apocleinae) females deposit their eggs on desert scrub, then cover them with a frothy material which hardens and protects them from desiccation. Thus, the thin-walled chorion in certain Asiliinae, Apocleinae, Dasypogoninae and Stichopogoninae/Stenopogoninae is derived, being adaptative in these environments because they are secondarily surrounded by moisture barriers (soil, plant, froth). Presumably, hatching here is delayed by the embryo entering dormancy, only to emerge during the rainy season. Alternatively, a thin-walled, smooth chorionic surface is pleisomorphic, with the Leptogastrine being the archiac group. The thick-shelled egg with an ornamented surface of

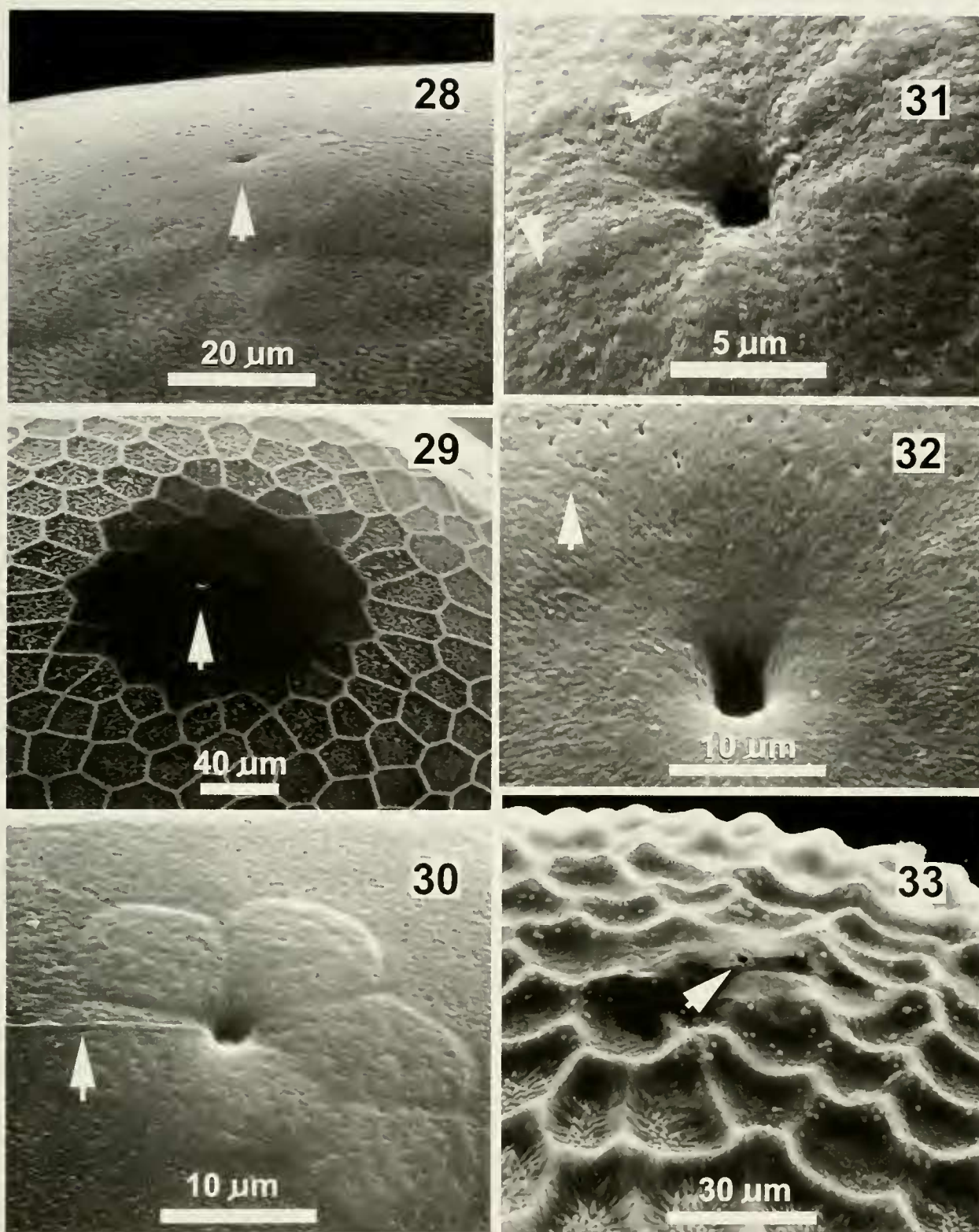
'forest' species would then be a derived character state.

Though factors influencing hatching of asilid eggs have yet to be studied, some environmental factors have been determined for lower Diptera, especially *Aedes* mosquitoes (Livdahl and Koenekoop 1985, Roberts 2001). Mature larvae hatch only when inundated with water in combination with rapid decreasing/increasing [oxygen and carbon dioxide] gas pressures. Thus, a critical change in gas pressures is probably a significant factor in hatching of eggs. Possibly asilid larvae in eggs, as well as pupae, respond similarly to changes in gas pressures when temporally submerged by water and may also explain the sudden emergence of adults in desert environments following the onset of the rainy season.

These results suggest that egg morphology may be useful to elucidate taxonomic and possibly phylogenetic relationships among asilids. The eggs of asilids may have a smooth or sculptured chorion. The specific pattern on the surface of egg chorions are imprints of the ovarian follicular cells which produce it (Chapman 1971). Significant differences in egg morphology of Palearctic *Dioctria flavipennis* and Nearctic *Eudioctria tibialis*, two related genera, are evident, especially in the oval and polygon patterns on the exochorion, the presence or absence of an eclosion line, construction of the ridges, presence or absence of interridge processes, and the distribution, abundance, and the structural configuration of aeropyles. Similarly, conspecific chorionic differences are also evident on the eggs of *Holcocephala abdominalis* and *H. calva*, several *Laphria* species, and those of *Cerostainia albipilosa* and *Atomosia puella*. Further studies on egg morphology of other species of *Dioctria* are anticipated and we hope those data will lend themselves to taxonomic separation of *Dioctria* species.

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Figs. 28–33. SEM micrographs of the micropylar area with a single micropyle on eggs of six asilid species from the mid-Atlantic region of North America. 28, *Atomosia puella* 29, *Laphria virginica*. 30, *Holcocephala abdominalis* showing floral-like micropylar region, sperm flagellum, and distribution of minute aeropyles. 31, *Holcocephala calva* showing minute aeropyles scattered around the micropyle. 32, *Endioctria tibialis* showing several minute aeropyles above the micropyle. 33, *Laphria flavicollis* showing low ridges surrounding the micropyle.

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